Received: 22 April 2020 | Revised: 18 August 2020 | Accepted: 21 August 2020

DOI: 10.1111/jbi.13982



RESEARCH PAPER

Journal of Biogeography | WILEY

# What drives diversification in a pantropical plant lineage with extraordinary capacity for long-distance dispersal and colonization?

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**Funding information**
B.A. Krukoff Fund For The Study Of African Botany; Ministerio de Ciencia e Innovación, Grant/Award Number: PGC2018-099608-B-I00; "la Caixa" INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centres of Excellence, Grant/Award Number: LCF/BQ/DI17/11620012

**Handling Editor:** Alain Vanderpoorten

## Abstract

**Aim:** Colonization of new areas may entail shifts in diversification rates linked to biogeographical movement (dispersification), which may involve niche evolution if species were not exapted to new environments. *Scleria* (Cyperaceae) includes *c*. 250 species and has a pantropical distribution suggesting an extraordinary capacity for long-distance dispersal and colonization. We investigate patterns of diversification in *Scleria*, and whether they are coupled with colonization events, climate niche shifts or both.

**Location:** Tropics and subtropics.

**Taxon:** Nutrushes *Scleria* (Cyperaceae).

**Methods:** We used molecular data from three DNA regions sequenced for 278 accessions representing 140 *Scleria* taxa (53% of species) to develop a chronogram, model ancestral ranges and measure rates of diversification. Integrating data from 12,978 digitized and georeferenced herbarium records, we investigated niche evolution.

**Results:** High dispersal rates in *Scleria*, a genus with multiple dispersal syndromes, make reconstruction of ancestral ranges at deep nodes in the phylogeny highly equivocal. Main dispersal and colonization events involve movements from South to Central America (*c*. 19), from Africa to Madagascar (*c*. 12), from Asia to Oceania (*c*. 7), from Africa to South America (*c*. 7) and Central America to South America (*c*. 6). The two main shifts in diversification rates happened during the warm period of the Miocene.

**Main conclusions:** Dispersification from South America to Africa without climate niche shift seems to explain the diversification shift in section *Hypoporum* implying that species were exapted. Shifts in climate niche evolution predate the second shift in diversification rates suggesting lineages were exapted prior to biogeographical movements. Within subgenus *Scleria*, colonizations of Asia and Madagascar by sections *Elatae* and *Abortivae*, respectively, are coupled with niche shifts suggesting that these colonizations involved climate niche adaptation.

KEYWORDS
ancestral range estimation, biogeography, Cyperaceae, dispersification, niche evolution, nutrushes

## 1 | INTRODUCTION

Clade-specific bursts in diversification rates have been associated with morphological changes termed key innovations related to novel niche invasions, increasing individual fitness or reproductive isolation (e.g. Naciri & Linder, 2020). Dispersification or 'key opportunity' has been defined as shifts in diversification rates associated with biogeographical movements without necessarily invoking key innovations (Donoghue & Sanderson, 2015; Moore & Donoghue, 2007; Uribe-Convers & Tank, 2015). Dispersification and key innovations do not exclude each other and shifts in diversification rates may be related to synergetic action of both (Moore & Donoghue, 2007).

After colonization, (a)biotic conditions may limit establishment of species. If species are unable to adapt to new environmental conditions (i.e. niche conservatism), they may only colonize environments similar to those in their original range (Pulliam, 2000). However, species can sometimes adapt to new environmental conditions (i.e. niche shifts, niche evolution), enabling colonization of new (a)biotic conditions (e.g. Pearman, Guisan, Broennimann, & Randin, 2008; Villaverde, González-Moreno, Rodríguez-Sánchez, & Escudero, 2017). A key innovation may allow a species to invade a new niche (novel niche invasion) allowing a subsequent shift in diversification rates (Boucher et al., 2012). In a scenario of dispersification (e.g. Donoghue, 2008), new environments reached after dispersal will often be colonized with lineages from environmentally similar areas (Moore & Donoghue, 2007). Alternatively, shifts in diversification rates have been associated with major historical climatic events (Erwin, 2009).

A family-wide biogeographical study of the sedge family Cyperaceae has shown that species-rich sedge clades are more widespread, occupy more niche space and diversify faster than species-poor lineages (Spalink et al., 2016). Here, we focus on a species-rich pantropical sedge clade, the genus *Scleria* P.J. Bergius (*c*. 250 species; Figure 1). The most diagnostic feature of nutrushes are the fruits called nutlets that characteristically have two cup-like structures at their base: the hypogynium and cupule (Figure 1g–i). Most *Scleria* species occur in the tropical zone below 1,600 m, with some extending into warm temperate regions (Bauters, 2018). In the tropics, species growing at higher elevations are also adapted to a more temperate climate than species growing in lowlands. Approximately 112 species are known from the Americas, 105 from Africa and 58 from Asia and Oceania. The pantropical distribution of *Scleria* suggests an extraordinary capacity for long-distance dispersal (LDD) and colonization. The dispersal unit of *Scleria*, that is the nutlet (plus hypogynium in most groups), are dispersed by different vectors. Abiotic dispersal via gravity and/or wind is common in species with unspecialized nutlets. Species of section *Ophryoscleria* have a corky-swollen cupule which stays attached to the nutlet, making it buoyant (Robinson, 1962). These species occur in very wet areas making hydrochory a likely mechanism. Biotic vectors have also been observed. *Scleria* nutlets are often reported to be dispersed by birds (Bauters, 2018 and references therein). Other authors have observed ant-mediated dispersal (Gaddy, 1986), most commonly in species with tubercle-like structures near the base of the nutlet (e.g. subgenus *Trachylomia*). While dispersal via gravity and/or wind and ant-mediated dispersal likely occurs over short distances, dispersal via water and birds may happen over long distances (LDD). Throughout their range, *Scleria* species occur in open places in forests, grasslands, road- and riversides, swamps, etc. (Bauters, 2018). Some species have local uses as medicines and materials (Simpson & Inglis, 2001), but they are not cultivated and have not purposefully been introduced outside their native distribution ranges. A few species have been reported as invasive (e.g. *Scleria lacustris* C.Wright in Florida; Jacono, 2001). Molecular phylogenetic studies (Bauters et al., 2016; Bauters, Goetghebeur, Asselman, Meganck, & Larridon, 2018) established a new infrageneric classification of *Scleria*, which enables us to investigate biogeography, diversification rate patterns and niche evolution in *Scleria*.

Important questions for macroevolution and biogeography do not have a clear answer yet. Why do some biogeographical movements and/or trait changes implicate shifts in diversification rates, whereas others do not (Moore & Donoghue, 2007)? In case of a shift in diversification rates, how often is it related to biogeographical movement (dispersification), trait change (key innovation), both or none? We hypothesize that shifts in diversification rates are significantly related with biogeographical movements and trait changes (niche shifts). In this study, we use the pantropical sedge genus *Scleria* to infer diversification rate patterns and their relationship with biogeographical movements (dispersification) and niche shifts (as a proxy of key innovation related to novel niche invasions).

## 2 | MATERIALS AND METHODS

### 2.1 | Taxon and data sampling

DNA sequence data of three markers (ITS, *ndhF*, *rps16*) generated in previous studies (Bauters et al., 2016, 2018; Galán Díaz, 2017; Semmouri et al., 2019) are used in this study. The sampling includes four species of tribe Bisboeckelereae, sister to tribe Sclerieae, and 140 accepted *Scleria* taxa (representing 53% of *Scleria* species). Approximately 48 of 112 (43%) American species (areas: South, Central and North America), 72 of 105 (69%) African species (Africa and Madagascar) and 20 of 58 (34%) Asian and Oceanian species (Eurasia and Oceania). Accessions sequenced per marker, ITS: 137, *ndhF*: 136, *rps16*: 135. Voucher information is provided in Table S1.

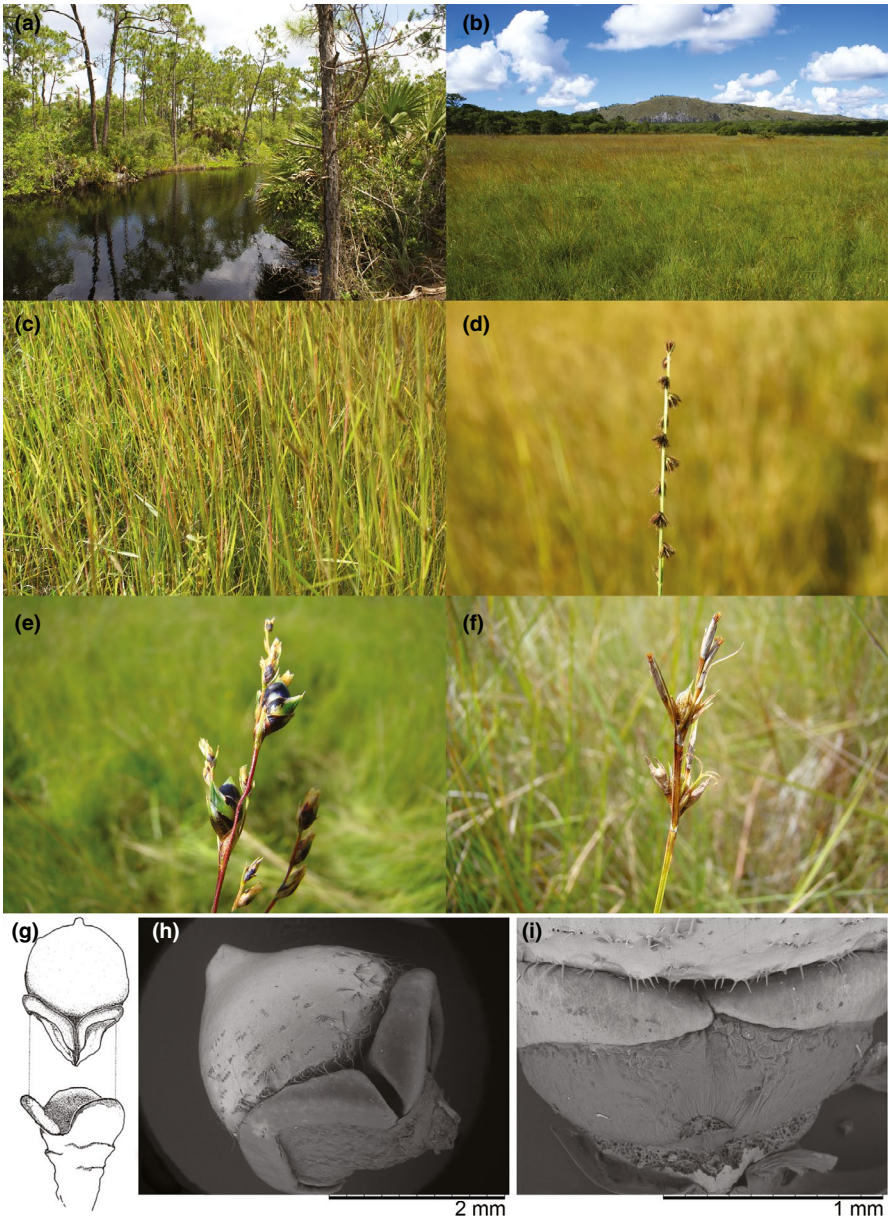


**FIGURE 1** *Scleria* habitats and morphology. (a) Swamp habitat of *S. baldwinii* (Torr.) Steud. and *S. georgiana* Core in Florida (Collier Seminole State Park, 28 July 2013) by Kenneth Bauters. (b) Dambo habitat of *S. greigiifolia* (Ridl.) C.B.Clarke, *S. melanomphala* Kunth and *S. rehmannii* C.B.Clarke in Zambia (Mutinondo Wilderness Area, Little Chipundu Dambo, 12 April 2015) by Kenneth Bauters. (c) Temporarily wet grassland (bas fond) habitat of *S. catophylla* C.B.Clarke in Guinea (near Labé, 25 October 2016) by Isabel Larridon. (d) Inflorescence of *S. catophylla* (*I. Larridon 91* K; near Labé, Guinea) by Isabel Larridon. (e) Inflorescence and nutlets of *S. greigiifolia* (*K. Bauters 2015–0423* GENT; Mutinondo Wilderness Area, Zambia) by Lari Merritt. (f) Inflorescence, flower and nutlet of *S. unguiculata* E.A.Rob. (*K. Bauters 2015–0413* GENT; Mutinondo Wilderness Area, Zambia) by Lari Merritt. (g) Nutlet of *S. gaertneri* Raddi with attached 3-lobed hypogynium; the 3-lobed cupule remains attached to the plant (adapted from De Wilde, 1998: figure 20). (h) SEM image of *S. williamsii* Gross with a 3-lobed hypogynium. (i) SEM image of *S. terrestris* (L.) Fassett showing the connection between the hypogynium (above, lighter grey) and the cupule (below, darker grey). SEM images by Kenneth Bauters

## 2.2 | Phylogenetic analyses and divergence time estimation

ITS, *ndhF* and *rps16* sequences were automatically aligned using Muscle (Edgar, 2004). Phylogenetic and divergence time estimations were performed in BEAST 2.4.5 (Bouckaert et al., 2014) using two GTR+I+G DNA substitution models for two independent partitions (nuclear versus. plastid DNA), a Birth-Death tree model, and an uncorrelated log-normal relaxed clock model (Drummond, Ho, Phillips, & Rambaut, 2006). We ran three independent analyses of 100 million generations. We evaluated mixing, convergence and stationary distribution using TRACER 1.7 (Rambaut, Drummond, Xie, Baele, & Suchard, 2018). Three calibration points, two secondary calibrations and one fossil calibration, were selected based on previous studies (Escudero & Hipp, 2013; Smith, Collinson, Rudall, & Simpson, 2010; Spalink et al., 2016). We calibrated the crown node of *Scleria* using the age of the oldest known fossil for the genus (Smith et al., 2010) with an offset of 33.8 Myr and standard deviation (*SD*) of 1.25 Myr. We applied a secondary calibration for the stem node of *Scleria* based on Spalink et al. (2016) with a mean of 57 Myr and *SD* of 2.5 Myr. Finally, we constrained the crown node of the sister group, tribe Bisboeckelereae, with a secondary calibration using a mean of 20 Myr and *SD* of 2.5 Myr (Escudero & Hipp, 2013). We applied a normal distribution prior to the secondary calibration points and a lognormal distribution prior to the fossil calibration point. Selected nucleotide substitution models were based on the maximum Akaike information criterion (AIC) weight resulting from the analysis of each DNA region in JMODELTEST 2.1.3 (Darriba, Taboada, Doallo, & Posada, 2012). TREEANNOTATOR 2.4.0 (Bouckaert et al., 2014) was used for reconstruction of the

maximum credibility tree, after removing the first 20% of trees in each run as burn-in.

## 2.3 | Biogeographical analyses

We inferred ancestral ranges using the R (R Core Team, 2019) package BioGeoBEARS (Matzke, 2013). We included seven areas in our analyses: South America, Central America, North America, Africa, Madagascar, Eurasia and Oceania (Table S2). We set these areas based on Dupin et al. (2017) with minor modifications considering peculiarities of our study group (specifically, we merged the Caribbean with Central America and we split Madagascar from Africa). The parameter maxareas was unconstrained. BioGeoBEARS implements two main models for large-scale biogeographical reconstruction: DIVA-like (Dispersal–Vicariance Analysis, Ronquist, 1997) and DEC (Dispersal–Extinction–Cladogenesis, Ree, Moore, Webb, & Donoghue, 2005; Ree & Smith, 2008). DEC and DIVA-like were also combined with the extra free parameter founder (j), which allows for cladogenetic dispersal, where the speciation event occurs in a different area than that of the ancestor. We also re-ran these four models incorporating into our models a matrix of dispersal connectivity corrected by a new free parameter w with temporal shifts in the potential dispersal connectivity (Dupin et al., 2017; Van Dam & Matzke, 2016). Our matrix of dispersal connectivity with temporal shifts is based on Dupin et al. (2017) with some minor modifications (because we removed one area from Dupin et al., 2017 –Caribbean– and added a new one –Madagascar). Finally, we compared the likelihoods of our data given all eight models using AICc. We compare the fit of DEC models against DIVA-like models. We also compared the fit of models including the free parameter w and dispersal connectivity that change through time against models without those. We did not compare models with j and without j parameter because the way j parameter enters into the model does not allow such comparison (Ree & Sanmartín, 2018). The results obtained with models that include the parameter j will be interpreted cautiously as they tend to overvalue the role of cladogenetic dispersal (j) at the cost of underestimating (d). We performed biogeographical stochastic mapping (BSM) analyses as implemented in Matzke (2014) and Dupin et al. (2017) to estimate the number and type of biogeographical events. We conducted BSMs using the best-fitting models (DEC+w and DEC+j+w, see results). Event frequencies were estimated by taking the mean and *SD* of event counts from 50 BSMs.

## 2.4 | Diversification pattern analyses

Patterns and shifts in diversification rates were estimated in Bayesian analysis of macroevolutionary mixtures (BAMM) using reversible-jump Markov chain Monte Carlo (rjMCMC) (Rabosky, 2014). The method allows changes in the numbers and locations of nodes at which speciation and extinction rates shift. All priors were set as recommended using the setBAMMpriors function (the analysis was conducted using a prior of one shift in diversification rates). The analysis was conducted assuming a global sampling fraction of 0.5 to account for missing taxa. The rjMCMC was run using Metropolis-coupling with four chains of five million generations each, saving trees every 1,000 generations. The R packages 'coda' (Plummer, Best, Cowles, & Vines, 2006) and BAMMtools (Rabosky et al., 2014) were used to check the Bayesian analysis and summarize and plot the results.

## 2.5 | Niche evolution analyses

To estimate the climatic niche of the taxa included in the phylogenetic analyses, a database of *Scleria* occurrences was built. All georeferenced entries of *Scleria* available on the Global Biodiversity Information Facility (GBIF, 2018) were downloaded. GBIF is the largest repository of digitized occurrences information, however, it is necessary to apply certain filtering steps to minimize error in posterior analyses (Spalink et al., 2016). First, we eliminated all duplicate records and corrected the taxonomy following Bauters et al. (2016, 2018) and Galán Díaz et al. (2019). Second, for each species, all occurrences were plotted and points falling outside its known range were manually excluded. Third, because spatial clustering as a result of sampling bias can influence climatic niche analyses, we randomly retained one point per species and per cell of a 2.5-min spatial resolution raster (about 4.5 km at the equator). Fourth, points were eliminated that were clearly outside the climatic range of the species. This was done by extracting the value of annual mean temperature and temperature annual range from WorldClim Global Climate Dataset 2.0 (Fick & Hijmans, 2017) for every point. Then, for every species and climatic variable, we retained points that were within 1.5 times the interquartile range. For steps three and four, cell-size and climatic threshold were established after several trials in order to retain as many points as possible while eliminating aberrant observations. Finally, the database was supplemented with records for collections not yet available on GBIF from herbaria such as BR, K, GENT, L, MO, NY, P, US and WAG (Thiers, continuously updated), which were georeferenced using Google Earth. A total of 12,978 records were used for posterior analyses. The average number of records per species is *c.* 93 (1–1,306; Table S3).

Bayesian reversible-jump multi-regime Ornstein–Uhlenbeck approach as implemented in the R (R Core Team, 2019) package 'bayou' (Uyeda & Harmon, 2014) was used to infer major shifts in niche evolution. This package implements an Ornstein–Uhlenbeck (OU) model to model trait evolution. This has two components, the stochastic and the deterministic component. The stochastic component is a Brownian Motion (BM) model which has a single parameter, sigma, which quantifies the rate of stochastic evolution of a given trait. The deterministic component has two parameters, theta and alpha. Theta is optimum towards the trait evolves and alpha is the rate of evolution towards the optimum. The OU model

estimates an overall sigma, theta and alpha and an additional theta value for the root of the phylogeny and for each inferred optimum shift. We ran the analyses for bio1 (annual mean temperature, °C*10), bio4 (temperature seasonality, °C*100), bio7 (temperature annual range, °C*10), bio12 (annual precipitation, mm) and bio 15 (precipitation seasonality, mm) which we believed are ecologically informative and amenable for interpretation. Nevertheless, we ran a hierarchical clustering analysis using the hclust function in R (R Core Team, 2019) to understand if the chosen five bioclimatic variables explain most the variation accumulated in the 19 available bioclimatic variables. We decided to add a sixth bioclimatic variable –bio18 (precipitation of warmest quarter)—to better represent the variation stored in the 19 bioclimatic variables. We set up the analyses following Pimiento, Cantalapiedra, Shimada, Field, and Smaers (2019). Three independent MCMC analyses of 2.5 million generations were run for each of the six bioclimatic variables. We used a burn-in of 30%.

In order to study the evolution of the whole niche rather than single bioclimatic variables, we calculated principal components using the function prcomp (scale was set as true) implemented in R (R Core Team, 2019). We studied the evolution of PC1, PC2 and PC3 using bayou (with the same options as for the single bioclimatic variables).

### 2.6 | Quantitative state speciation and extinction

In order to model niche evolution and diversification rates, we used the model QuaSSE (FitzJohn, 2010) as implemented in diversitree (FitzJohn, 2012). We modelled the relationship between trait evolution and extinction rates as constant and the relationship between trait evolution and speciation as constant, linear, sigmoid and hump (FitzJohn, 2010). We modelled the trait evolution as a Brownian motion and Ornstein-Uhlenbeck models. In summary, for each of the bioclimatic variables and the three principal components we used eight models: BM.constant.constant, OU.constant.constant, BM.linear.constant, OU.linear.constant, BM.sigmoid.constant, OU.sigmoid.constant, BM.hump.constant and OU.hump.constant. Model selection was performed using AIC.

### 2.7 | Testing hypotheses of clade-specific diversification rates with BayesRate

We used the function 'Clade-specific rates' implemented in BayesRate (Silvestro, Schnitzler, & Zizka, 2011). We tested the hypothesis that clades that underwent a niche shift based on bayou results have different rates of diversification against the null hypotheses of (i) no shifts in diversification rates; and (ii) a single diversification rate shift in section *Hypoporum* (based on BAMM results). In order to test such hypotheses, we divided the phylogenetic tree in seven clades (background, section *Hypoporum*, subgenus *Trachylomia*, subgenus *Scleria*, section *Abortivae*, section *Elatae* and core section *Foveolidia*) and conducted four BayesRate analyses: (i) the seven clades are linked with the same rate of diversification; (ii) section *Hypoporum* evolves at a different rate than the other six clades; (iiia) section *Hypoporum* and the background evolve at one rate and the other five clades have five different diversification rates and (iiib) section *Hypoporum* and the background evolve at one rate and the other five clades evolve at another different rate. We also tested the hypothesis of that the clades that have suffered an ancestral range shift (based on BioGeoBEARS results) have different rates of diversification against the null hypotheses of (i) no shifts in diversification rates; and (ii) a single diversification rates shift in section *Hypoporum* (based on BAMM results) or two diversification rates shifts in section Hypoporum and section Elatae subclade 1 (based on BAMM results). In order to test such hypotheses, we divided the phylogenetic tree in eleven clades (subgenus *Browniae*, section *Lithospermae* plus *Virgatae*, section *Hypoporum*, subgenus *Trachylomia*, section *Corymbosae*, section *Margaleia* plus *Acriulus*, section *Melanomphalae* plus *Hymenolytrum*, section *Foveolidia* plus *Naumannianae*, sections *Elatae*, section *Ophyoscleria* plus *Scleria* plus *Schizolepis* and section *Abortivae*) and assigned five different diversification rates based on the ancestral range (Oceania, America, Africa, Asia and Madagascar) and conducted four additional BayesRate analyses: (i) the 11 clades are linked with the same rate of diversification; (iia) section Hypoporum evolves at a different rate than the other 10 clades; (iia) there are two shifts in diversification rates, one in section *Hypoporum* and another in section *Elatae* subclade1 and (iii) the 11 clades evolves at five different diversification rates depending on the ancestral range (subgenus *Browniae* in Oceania, section *Lithospermae* plus *Virgatae* in America, section *Hypoporum* in Africa, subgenus *Trachylomia* in America, section *Corymbosae* in Asia, section *Margaleia* plus *Acriulus* in Africa, section *Melanomphalae* plus *Hymenolytrum* in America, section *Foveolidia* plus *Naumannianae* in Africa, section *Elatae* in Asia, section *Ophyoscleria* plus *Scleria* plus *Schizolepis* in America and section *Abortivae* in Madagascar). All analyses were run for 500,000 iterations after a burn-in period of 50,000 iterations. Parameter values were sampled each 500 iterations. We compared the posterior probability of all hypotheses using BayesFactor.

## 3 | RESULTS

### 3.1 | Phylogenetic analyses and divergence time estimation

*Scleria* split from its sister lineage *c*. 55.3 Ma (Table 1; Figure S1). The crown age of *Scleria* was retrieved as *c*. 43.4 Ma. In *Scleria*, subgenus *Browniae* is sister to the rest of the genus. The crown age of subgenus *Brownieae* is very young (*c*. 3.9 Ma). The crown age for subgenus *Hypoporum* was estimated at *c*. 20.9 Ma, with its three sections diversifying more recently. The crown age of the subgenus *Trachylomia*+subgenus *Scleria* clade is *c*. 31.6 Ma, with the former being *c*. 6.9 Ma and the latter *c*. 25.5 Ma. Most of the species

**TABLE 1** Ages of the main *Scleria* lineages. Median node age and 95% of highest posterior density are shown in Ma

| Node (crown age) | Median node age | 95% highest posterior density |
|---|---|---|
| genus *Scleria*+Bisboeckelerae | 55.27 | 50.36–59.99 |
| genus *Scleria* | 43.44 | 33.93–54.05 |
| subgenus *Browniae* | 3.94 | 1.48–6.87 |
| subgenus *Hypoporum* | 20.89 | 12.26–30.17 |
| sect. *Hypoporum* | 8.4 | 5.22–11.74 |
| subgenera *Trachylomia*+*Scleria* | 31.58 | 22.70–40.87 |
| subgenus *Trachylomia* | 6.87 | 3.05–11.12 |
| subgenus *Scleria* | 25.53 | 17.61–33.34 |
| sect. *Corymbosae* | 22.28 | 14.47–30.49 |
| sect. *Margaleia* | 9.57 | 3.70–15.49 |
| sect. *Acriulus* | 13.88 | 8.62–19.76 |
| sect. *Hymenolytum* | 6.46 | 3.58–9.98 |
| sect. *Foveolidia* | 10.22 | 6.47–14.40 |
| sect. *Elatae* | 4.25 | 2.16–6.59 |
| sect. *Abortivae* | 5.63 | 3.54–7.96 |
| sect. *Schizolepis* | 4.22 | 2.47–6.20 |
| sect. *Scleria* | 2.07 | 0.60–3.96 |
| sect. *Ophryoscleria* | 5.76 | 3.63–8.18 |

diversity within subgenus *Scleria* has arisen in the last *c*. 5 Ma, except in sections *Acriulus* and *Margaleia* where the lineages appear older.

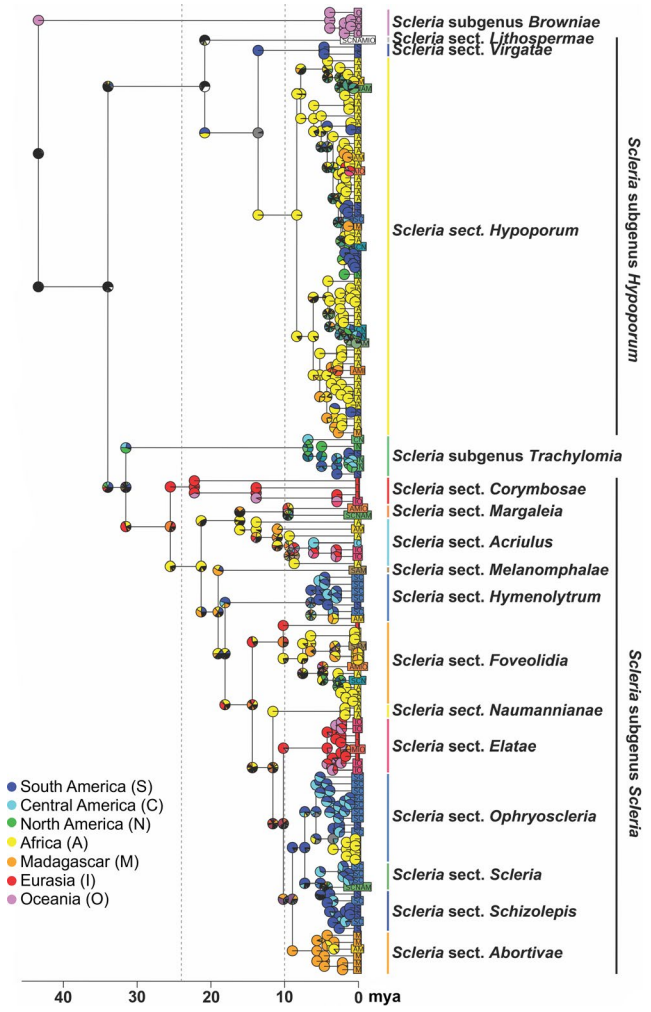


**FIGURE 2** DEC+w dated biogeographical reconstruction. We included seven areas in our analyses: South America (S, dark blue), Central America (C, pale blue), North America (N, green), Africa (A, yellow), Madagascar (M, orange), Eurasia (I, red) and Oceania (O, pink). The pie charts represent probabilities of states/ranges at each node. Time in million years ago (Ma). Subgenera and sections are indicated with vertical bars. For the DEC+w+j reconstruction see Figure S2

## 3.2 | Ancestral range estimations

To find the best model in BioGeoBEARS, we compared unconstrained versus constrained models, and DEC versus DIVA-like models. The fit (smaller AICc) was significantly better for constrained and DEC models, accordingly, we selected DEC+w and DEC+w+j as the best models (Table 2). The high dispersal rates inferred for *Scleria* make reconstruction of ranges for deep nodes of the phylogeny as highly equivocal (Figure 2; Figure S2). Main dispersal and colonization events involve movements (in decreasing order) from South to Central America (*c*. 19), from Africa to Madagascar (*c*. 12), from Asia to Oceania (*c*. 7), from Africa to South America (*c*. 7) and Central America to South America (*c*. 6) (Figures 3 and 4; Table 3).

**TABLE 2** BioGeoBEARS models comparison. Likelihood, number of parameters, parameters (d, e, j and w) and AICc are shown. The best models are in bold

| | LnL | n params | d | e | j | w | AICc |
|---|---|---|---|---|---|---|---|
| DEC | −388.5 | 2 | 0.018 | 0.0009 | – | – | 781.1 |
| DEC+j | −384.2 | 3 | 0.017 | 3.7e−09 | 0.0092 | – | 774.5 |
| DIVA-like | −393.6 | 2 | 0.020 | 2.0e−09 | – | – | 791.3 |
| DIVA-like+j | −391.6 | 3 | 0.019 | 1.0e−12 | 0.0054 | – | 789.3 |
| **DEC+w** | **−380** | **3** | **0.036** | **1.0e−12** | **–** | **0.50** | **766.2** |
| **DEC+j+w** | **−376.6** | **4** | **0.030** | **1.0e−12** | **0.015** | **0.43** | **761.5** |
| DIVA-like+w | −387.1 | 3 | 0.032 | 1.0e−12 | – | 0.31 | 780.3 |
| DIVA-like+j+w | −384.2 | 4 | 0.035 | 1.0e−12 | 0.0086 | 0.43 | 776.7 |

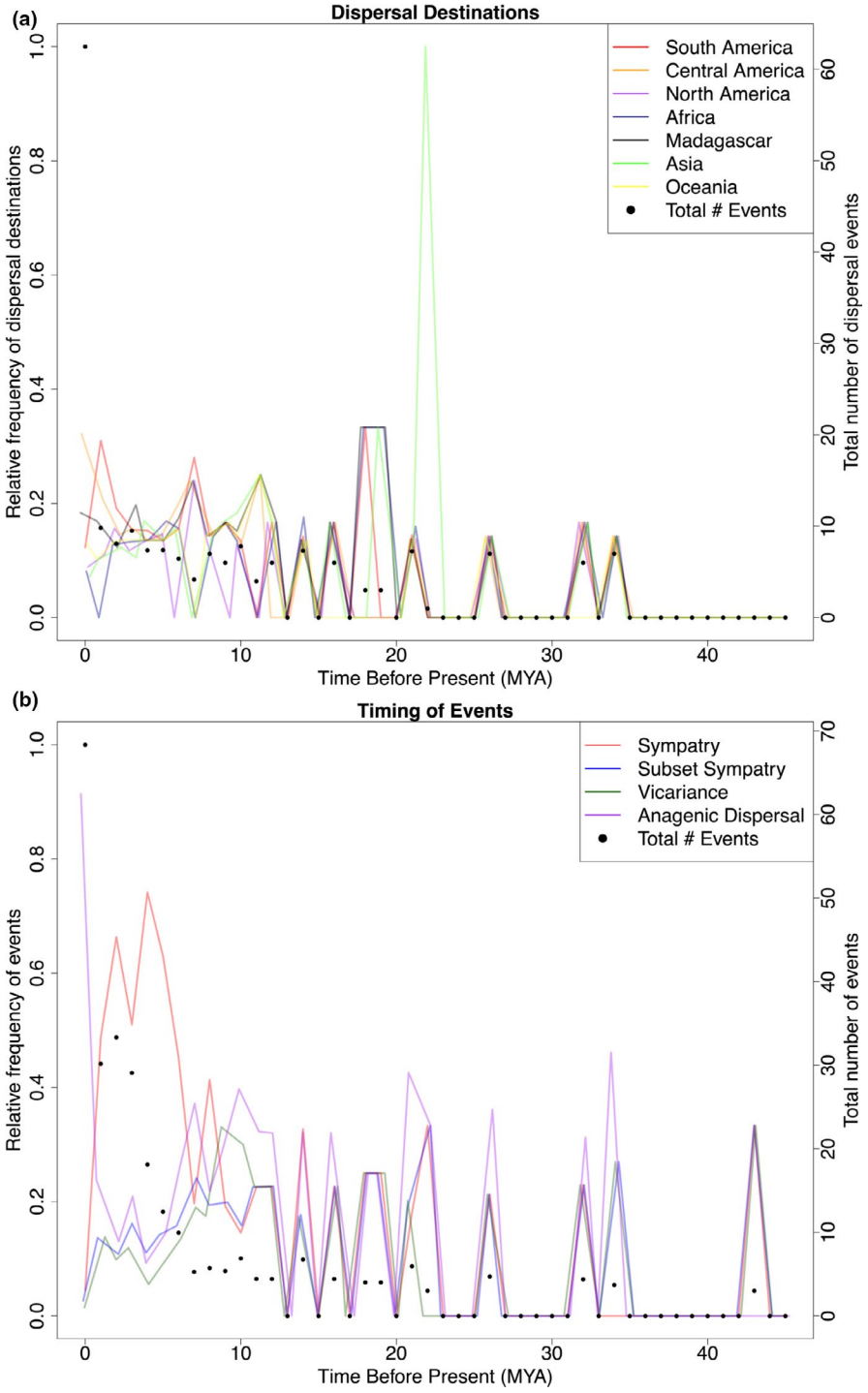


**FIGURE 3** Timing, type, destination and frequency of dispersal events in the ancestral area reconstruction (BSM DEC+w). (a) Timing, destination and frequency: Each colour represents one of the eight defined geographical regions, illustrated by the legend at the top of the figure. The total number of events is indicated by a black bullet (•). (b) Timing, type and frequency: (narrow) within-area speciation (red), subset within-area speciation (blue), vicariance (green) and anagenic dispersal (purple). The total number of events is indicated by a black bullet (•). For the BSM DEC+w+j summaries see Figure S3

## 3.3 | Diversification patterns

We found that five very similar scenarios accumulated 0.98 of posterior probability (PP, from the best to worst: 0.32, 0.29, 0.20, 0.12 and 0.057; Figure 5; Figure S4, Table S5). The four best scenarios (which sum a total PP of 0.93) find a positive shift in diversification rates in section *Hypoporum*. The second, third and fourth scenarios (which sum a total PP = 0.61) also agree in a second positive shift in diversification rates but there is some uncertainty in the specific location of this second diversification rate shift. The second-best scenario (Figure 5a) included in this second shift in diversification rates seven sections of subgenus *Scleria* (sections *Ophryoscleria*, *Scleria*, *Schizolepis*, *Abortivae*, *Elatae*, *Naumannianae* and *Foveolidia*). We have termed this clade subgenus *Scleria* subclade 1. The third and the fourth best scenarios include section *Hymenolytrum* and sections *Hymenolytrum* and *Melanomphalae*, respectively, in the clade that undergoes the shift (Figure S4). We infer two main changes in the diversification pattern during the warm period of the Miocene, a sudden increase in diversification rates located in section *Hypoporum* and

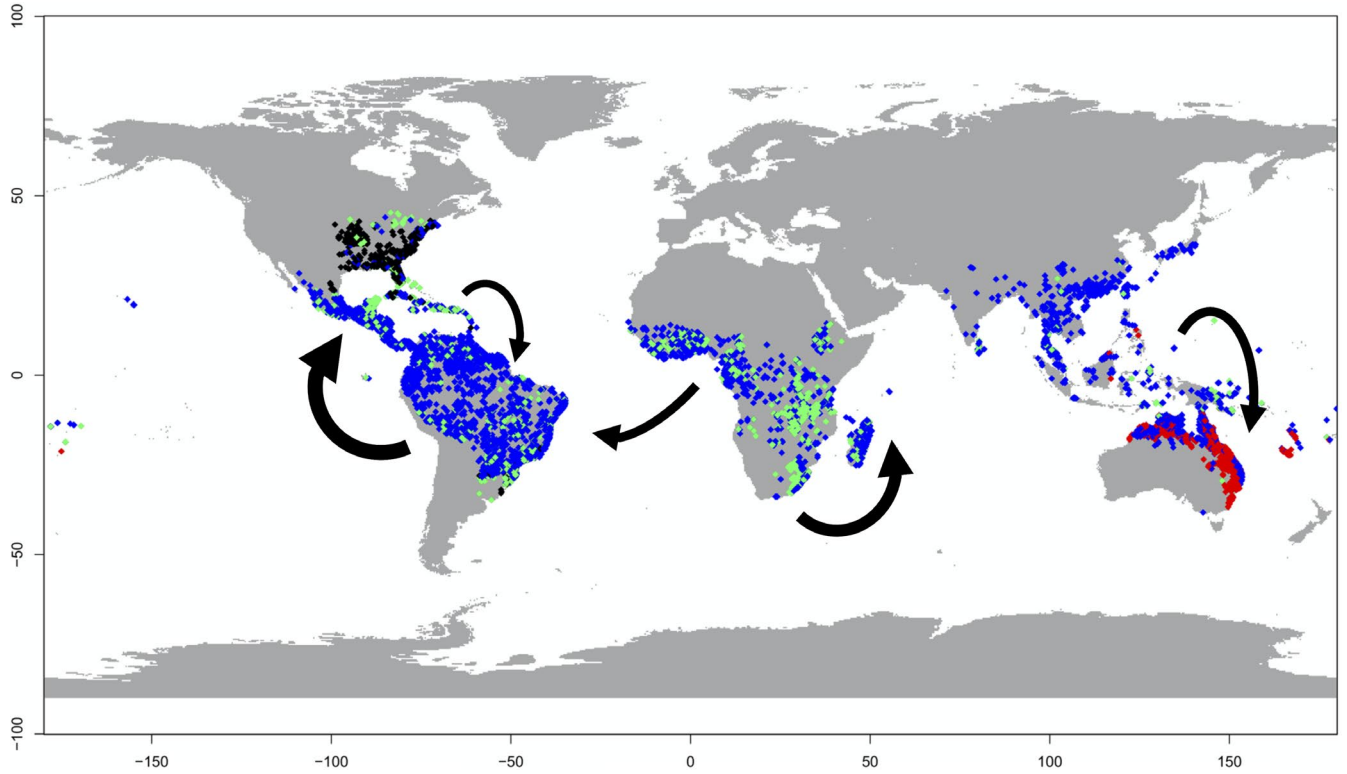


**FIGURE 4** Map of the pantropical distribution of *Scleria*. Species distribution is coloured by subgenus (red = *Browniae*; green = *Hypoporum*; black = *Trachylomia*; blue = *Scleria*), showing the main movements from the BSM DEC+w BioGeoBEARS analysis. Equirectangular projection, note that the scale varies across the map

a second sudden increase in subgenus *Scleria* of which the location is partially equivocal.

### 3.4 | Niche evolution

For all analyses, we obtained effective sizes for our Bayesian models >100. We report only the shifts with a PP >0.30. For details see Figure S5 and Table S6. Annual mean temperatures (bio1) showed low rates of stochastic evolution and high rates of evolution towards the optima. We inferred two shifts of optima for bio1 (Figure 6a): in subgenus *Trachylomia* (PP = 0.56) and in subgenus *Scleria* (PP = 0.35). There is a shift from higher to lower optimum in annual mean temperatures in subgenus *Trachylomia* and the opposite in subgenus *Scleria*. Temperature seasonality (bio4) showed high rates of stochastic evolution and high rates of evolution towards the optima. For bio4, we obtained one optimum shift in subgenus *Trachylomia* (PP = 0.997). This shift is from lower to higher optimum in temperature seasonality. Annual range of temperature (bio7) showed low rates of stochastic evolution and high rates of evolution towards the optima. For bio7, we obtained two shifts (Figure 6b): in subgenus *Trachylomia* (PP = 0.91) and in subgenus *Scleria* (PP = 0.36). There is a shift from lower to higher optimum in annual range of temperatures in subgenus *Trachylomia* and the opposite in subgenus *Scleria*. Annual precipitation (bio12) showed low rates of stochastic evolution and low rates of evolution towards the optimum. For bio12, we obtained no shift with PP > 0.30. Precipitation seasonality (bio15) showed low rates of stochastic evolution and low rates of evolution towards the optimum. For bio15, we obtained one optimum shift in subgenus *Trachylomia* (PP = 0.46). This shift is from higher to lower optimum in precipitation seasonality. Precipitation of the warmest quarter (bio18) showed low rates of stochastic evolution and very high rates of evolution towards the optima. For bio18, we obtained four optimum shifts (Figure 6c): in section *Abortivae* (PP = 0.95), in section *Elatae* (PP = 0.56), in a small clade within section *Hypoporum* (PP = 0.53) and in core section *Foveolidia* (PP = 0.35). In section *Abortivae*, section *Elatae* and the small clade within section *Hypoporum*, there are shifts from lower to higher optimum in precipitation of warmest quarter. However, in core section *Foveolidia* the shift is from higher to lower optimum in precipitation of the warmest quarter. The niche shifts related to subgenus *Scleria*, subgenus *Trachylomia* and the sections in subgenus *Scleria* occurred *c*. 30 Ma, *c*. 20 Ma and *c*. 7–9 Ma respectively. The shift in subgenus *Scleria* is from more temperate to a more tropical climatic regime, whereas that in subgenus *Trachylomia* is from a tropical to a more temperate climatic regime in temperature (lower temperature, higher range and seasonality) but the opposite in precipitation (less seasonality). In the sections of subgenus *Scleria*, the shifts are both to a more tropical climatic regime (sections *Abortivae* and *Elatae*) and to a more temperate climatic regime (core section *Foveolidia*). Because *Scleria* species grow only in tropical areas (see Figure 1) the species and clades with a more temperate climatic regime are

**TABLE 3** Summary of the number of dispersal events (and standard deviations, *SD*) between the different considered regions (sources of dispersal in rows and sinks of dispersals in columns) inferred by the BSM analysis under the DEC+w model. The main movements are in bold. For the events inferred under the DEC+w+J model, see Table S4

| | | | To | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | South America | Central America | North America | Africa | Madagascar | Eurasia | Oceania |
| From | South America | Mean (*SD*) | – | **19.32 (2.80)** | 2.9 (1.13) | 2.5 (1.33) | 2.56 (1.09) | 0.5 (0.91) | 0.18 (0.39) |
| | Central America | Mean (*SD*) | **5.72 (3.04)** | – | 3.24 (1.49) | 0.54 (0.61) | 0.5 (0.61) | 0.28 (0.61) | 0.28 (0.50) |
| | North America | Mean (*SD*) | 2.26 (1.17) | 3.84 (1.57) | – | 1.14 (0.93) | 0.64 (0.80) | 0.28 (0.50) | 0.08 (0.27) |
| | Africa | Mean (*SD*) | **6.98 (1.66)** | 2.34 (1.21) | 2.5 (1.13) | – | **12.12 (2.07)** | 4.46 (1.57) | 1.96 (1.05) |
| | Madagascar | Mean (*SD*) | 1.56 (0.95) | 0.94 (0.84) | 0.50 (0.71) | 3.96 (1.94) | – | 0.88 (0.87) | 0.60 (0.67) |
| | Eurasia | Mean (*SD*) | 0.44 (0.67) | 0.50 (0.58) | 0.28 (0.50) | 1.38 (1.16) | 1.26 (0.99) | – | **7.48 (1.68)** |
| | Oceania | Mean (*SD*) | 0.28 (0.50) | 0.24 (0.42) | 0.16 (0.82) | 0.68 (0.65) | 0.70 (0.65) | 2.06 (1.43) | – |

typical of highlands and the ones with a more tropical climatic regime are typical of lowlands.

The results from the analyses of evolution of PC1, PC2 and PC3 (Figure S6, Table S6) were very similar to the ones obtained using the individual bioclimatic variables. We inferred a single shift in PC1 in subgenus *Scleria*. We inferred no shifts for PC2. And we inferred two shifts for PC3, one in subgenus *Trachylomia* and one in section *Abortivae*. Although results from principal components are more difficult to interpret than from single bioclimatic variables, the results seem to suggest a shift to a more tropical climate regime in subgenus *Scleria* and sect. *Abortivae*, and a shift to a more temperate climate regime in subgenus *Trachylomia*.

## 3.5 | Quantitative state speciation and extinction

For all bioclimatic variables, the models BM.constant.constant and OU.constant.constant are significantly rejected. The bioclimatic variables bio1, bio7 and bio15 follow a BM process and the bioclimatic variables bio4, bio12 and bio18 an OU process. Whereas bio1, bio7, bio15 and bio18 seem to better modelled by a hump.constant model in which speciation rates are highest at mid values, bio4 and bio12 seem to be better modelled by a sigmoid.constant model in which speciation rates are the highest at high values and decrease suddenly at certain point (Table S7; Figure S7). For the principal components, the models BM.contant.contant and OU.constant.constant are also significantly rejected. PC2 follows a BM process, whereas PC1 and PC3 follow an OU process. The principal components seem to better modelled by a hump.constant model in which speciation rates are highest at mid values (Table S8).

## 3.6 | Testing hypotheses of clade-specific diversification rates with BayesRate

Regarding hypotheses of diversification rates linked to niche shifts (Table S9), BayesRate analyses significantly support a single diversification rate shift in section *Hypoporum* (cf. the single best supported scenario in BAMM analyses). Nevertheless, different diversification rates associated with niche shifts are significantly supported when compared to the null hypothesis of a single rate of diversification (specifically, the modes of different rates associated to different niche is marginally supported over the option of a single rate for all clades with niche shift).

Regarding hypotheses of diversification rates linked to biogeographical movements, BayesRate analyses significantly support the hypothesis that diversification rates are linked to ancestral ranges of the clades. This hypothesis is significantly supported over the hypotheses associated to BAMM results. Nevertheless, the hypothesis of two shifts of diversification based on BAMM results, BF = 4.167, is only moderately worse. The other two null hypotheses, one rate of diversification or one shift in section *Hypoporum*, are strongly rejected.

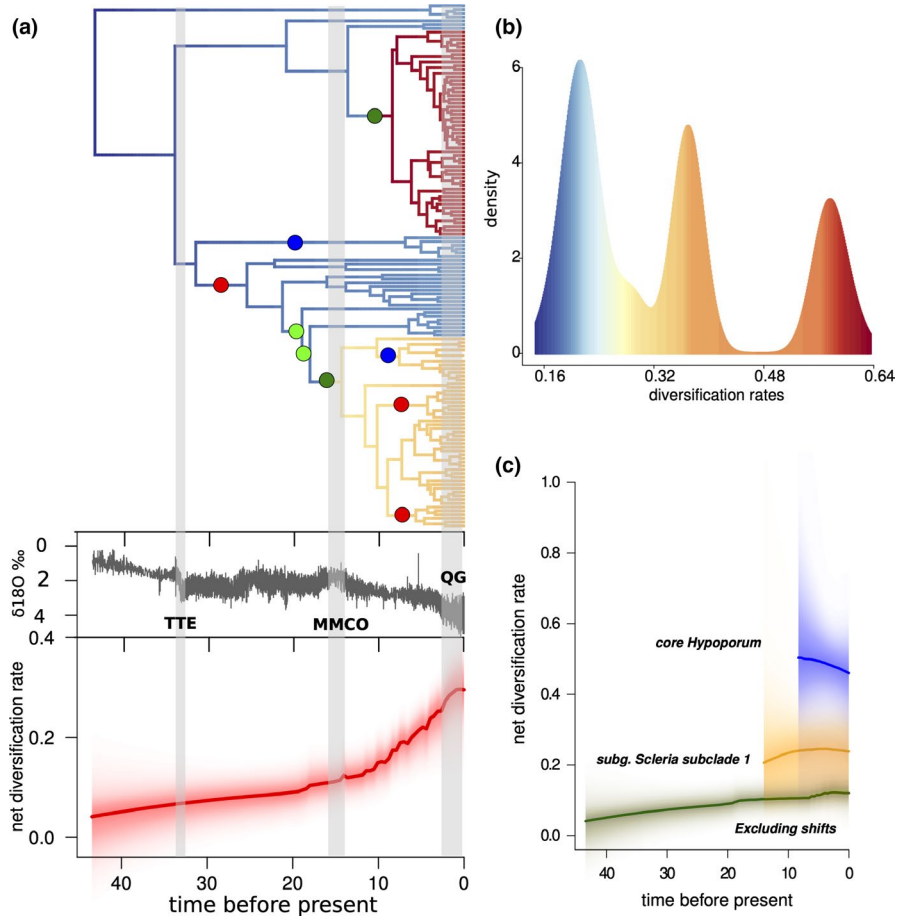


**FIGURE 5** Summary figure including results of the BAMM analyses showing diversification rates in species per million years and position of niche shifts. (a) Second-best BAMM scenario, with branch colours indicating diversification rates (see histogram in b), $^{18}O$ isotope reconstruction based on Lisiecki and Raymo (2005) in ‰ and diversification rates of all *Scleria*. Dark green dots indicate shifts in diversification rates, light green dots indicate alternative shifts in diversification rates in subgenus *Scleria* retrieved in the third and fourth best BAMM scenarios. Red dots indicate niche shifts towards a more tropical climatic regime and blue dots indicate niche shifts towards a more temperate climatic regime obtained in the results of the bayou analyses. (b) Histogram of frequency of diversification rates with colours confer the branches in the phylogeny, (c) Diversification rates of subgenus *Scleria* subclade 1, Core subgenus *Hypoporum* and excluding shifts. Abbreviations: Terminal Eocene Event (TTE), mid-Miocene Climatic Optimum (MMCO) and Quaternary Glaciations (QG). Timing of TTE, MMCO and QG are indicated with vertical grey bars

## 4 | DISCUSSION

### 4.1 | Are shifts in diversification rates linked to biogeographical movements?

We have inferred many biogeographical movements in *Scleria* (*c*. 103), most of them among relatively well connected areas (e.g. from South to Central America and vice versa *c*. 19 and 6, from Africa to Madagascar *c*. 12, from Asia to Oceania *c*. 7), but other events involving very unconnected areas (from Africa to South America *c*. 7). This massive number of dispersal and colonization events entail a high rate of dispersal that makes the estimation of ancestral ranges at deep nodes of the phylogeny equivocal. In Cyperaceae, a study of tribe Schoeneae, which is largely distributed in the Southern Hemisphere, equally recovered a high number of transoceanic dispersal events (Viljoen et al., 2013). Most other biogeographical studies of Cyperaceae focussed on the temperate megadiverse genus *Carex* L. (*c*. 2,000 species), either investigating distribution patterns in *Carex* groups (e.g. Maguilla, Escudero, & Luceño, 2018), or recently in the genus as a whole (Martín-Bravo et al., 2019). Although high dispersal and colonization ability has been also inferred for *Carex*, the inferred dispersal rates were markedly lower ($d = 0.0119$ events/my in Martín-Bravo et al., 2019 against $d = 0.036$ events/my in this study). Furthermore, most dispersal events in *Carex* occur between areas in the Northern Hemisphere, which are much more connected than tropical areas. If we compare dispersal and colonization ability of just the tropical lineages of *Carex* to the pantropical genus *Scleria*, then *Scleria* stands out even more as a high disperser. When we compare dispersal rates in *Scleria* with those in Cyperaceae overall (Spalink et al., 2016), dispersal rates are higher in *Scleria*. This is also true when we compare with other plant lineages, at genus (Chomicki & Renner, 2016; Echeverría-Londoño, Särkinen, Fenton, Purvis, & Knapp, 2020; Yao, Song, Yang, Tan, & Corlett, 2020) or family level (Dupin et al., 2017). Interestingly, in the analyses of tribes of

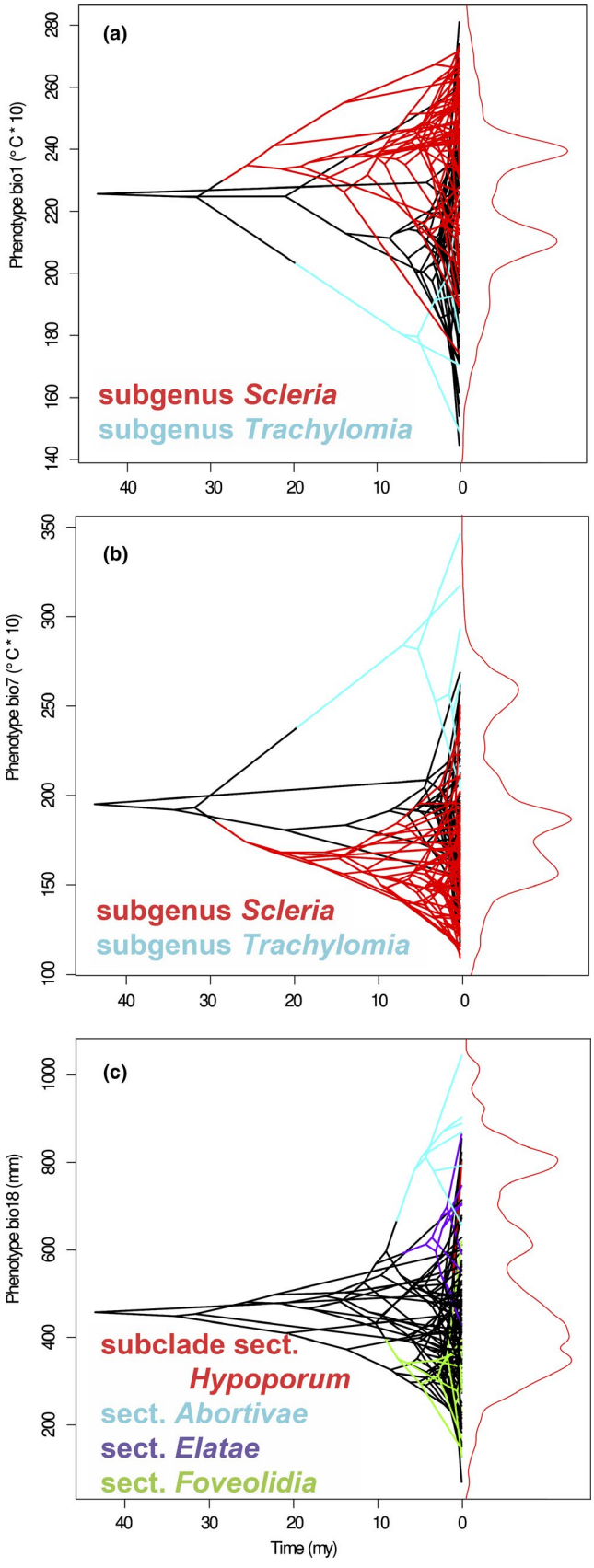


**FIGURE 6** Niche evolution. (a) Phenotype bio1, (b) Phenotype bio7, (c) Phenotype bio18. Time in millions years from the origin of the genus *Scleria* to present is shown on the x axis. Evolution of the phenotype of bio1 (in °C*10), bio7 (in °C*10) and bio18 (in mm) is shown on the y axis. The evolution of phenotypes of species, nodes and branches across time and the phylogenetic relationships are plotted. Black branches indicate ancestral optimum and optima shifts are indicated with different colours. The name of each clade with an optimum shift is indicated with a colour matching with the colour of the branches

Poaceae, a family with a similar graminoid habit, Hackel et al. (2018) found lower rates of dispersal in some tribes but higher rates of dispersal in others.

Contrarily to the large number of biogeographical movements, we only identified two shifts in diversification rates associated with them. This indicates that dispersal into new areas most often does not entail a shift in diversification rates. We hypothesize here that the synergetic action of biogeographical movements and key innovations might have triggered a shift in diversification rates in the two inferred dispersification processes. Dispersification from South America to Africa seems to explain the shift in section *Hypoporum*. The second shift in diversification rates (in subgenus *Scleria* subclade 1), with equivocal location, is related to biogeographical movements between Africa, Madagascar, South America and Asia. More detailed studies are needed to properly test these hypotheses of dispersification linked to key innovations related to increased individual fitness and/or reproductive isolation. Alternatively, the presence of a stochastic component, that is the impact of dispersal on diversification rates depends on being in the right place at the right time (Moore & Donoghue, 2007), may play a role. Despite most of biogeographical movements not being coupled with shifts in diversification rates, our clade-specific diversification rate analyses suggest that these biogeographical movements have indeed shaped the diversification process in genus *Scleria* as the clade partitioned analysis based on ancestral range received the highest support, even over the clade partitioned analysis based on BAMM results.

## 4.2 | Are shifts in diversification rates linked to major historical climatic events?

The evolutionary history of *Scleria* stretches back to *c.* 50 Ma. Major historical climatic events in this time frame include the Early-Eocene Climatic Optimum (EECO, *c.* 52.6–50.3 Ma), during which Earth was dominated by tropical biomes even at high latitudes (Morley, 2003). After the EECO, the most important climatic events were the Terminal Eocene Event (TTE) and the Mid-Miocene Climatic Optimum (MMCO) (Zachos, Pagani, Sloan, Thomas, & Billups, 2001). The TTE (*c.* 34 Ma) coincides with a critical drop in global temperatures and a great expansion of arid vegetation. The MMCO (*c.* 14–16 Ma) matches with Earth's most recent prolonged warming event which allowed a new expansion of tropical biomes. From the Pliocene and Pleistocene (including Quaternary glaciations, *c.* 0.01–2.58 Ma), Earth has experienced lower global temperatures (Zachos et al., 2001). Shifts in diversification rates associated with major historical climatic events can entail

major extinctions in some clades, whereas diversification bursts can occur in others (Erwin, 2009). In *Hypericum* (Hypericaceae), in which two diversification rate shifts postdate the MMCO, climate cooling was suggested to explain, at least partially, the distribution pattern (mountains in the Tropics) and species-richness (Nürk, Uribe-Convers, Gehrke, Tank, & Blattner, 2015). In Cyperaceae, a similar pattern was found in *Carex* (Escudero & Hipp, 2013; Escudero, Hipp, Waterway, & Valente, 2012) in which a shift in diversification rates in the Core Carex Clade has been suggested to be related to global cooling since the Oligocene. In the case of *Scleria*, its origin in the Eocene (*c*. 44 Ma) was after the EECO when the temperatures were still relatively high and before the TTE with its critical drop in temperatures. During this period, diversification rates of *Scleria* were low which might be explained by high extinction rates as result of the interaction between a tropical lineage and a context of sudden climate change towards global cold temperatures. The shift in diversification rates of subgenus *Scleria* subclade 1 (*c*. 16 Ma) might be related to the warm period MMCO. Nevertheless, the location of this shift in diversification rates was not inferred with high confidence and it could have happened several millions of years before the MMCO. In addition, the shift in section *Hypoporum* (*c*. 10 Ma) is clearly unrelated to these three major climatic events and happened during a period of decreasing global temperatures. Consequently, historical climate changes explain, at most, only part of the diversification rate patterns found in *Scleria*.

### 4.3 | Are dispersification events linked to niche evolution?

Our inferred niche shifts cannot be considered key innovations as none of the five inferred clades with niche shifts matches with the two inferred shifts in diversification rates. Nevertheless, QuaSSE analyses clearly support a relationship between the bioclimatic variables (and principal coordinates) and diversification rates. This means that although niche shifts do not provoke shifts in diversification rates, niche evolution is indeed shaping the diversification process in *Scleria*. This is also supported by our clade-specific diversification rate analyses, since, although the partition based on BAMM results is the most supported one, the partitions based on niche shifts were significantly supported in comparison with a single diversification rate regime.

Dispersification may couple synergistically with key innovations (Moore & Donoghue, 2007). Whereas the inferred niche shifts in *Scleria* (*c*. 30 Ma in subgenus *Scleria* towards a more tropical climatic regime, *c*. 20 Ma in subgenus *Trachylomia* towards a more temperate climatic regime and *c*. 7–9 Ma in several sections within subgenus *Scleria* towards both more temperate and more tropical climatic regimes) neither match major historical climatic events, nor inferred dispersification events. In this way, dispersification from South America to Africa without a climate niche shift seems to explain the shift in diversification rates in section *Hypoporum* suggesting that species were exapted. Shifts in climate niche evolution predate the second shift in diversification rates which suggest these were also exapted Nevertheless, within this clade (subgenus *Scleria*), the colonizations of Asia and Madagascar by sections *Elatae* and *Abortivae*, respectively, are coupled with two niche shifts suggesting that these colonizations involved the coetaneous climate niche adaptation of these clades but without subsequent shifts in diversification rates.

### 4.4 | Final remarks

We found high dispersal rates in *Scleria*, a genus with multiple dispersal syndromes. Shifts in diversification rates in *Scleria* are related either to biogeographical movement, or to both biogeographical movement and major historical climate events. However, shifts in diversification rates seem unrelated to niche transitions. Our results do not conclusively answer the question of why some biogeographical movements and/or trait changes implicate shifts in diversification rates, whereas others do not.

#### ACKNOWLEDGEMENTS

IL is supported by the B.A. Krukoff Fund For The Study Of African Botany. M.E. is supported by the Spanish Ministry of Science and Innovation through the project PGC2018-099608-B-I00. J.G.D. has received financial support through the 'la Caixa' INPhINIT Fellowship Grant for Doctoral studies at Spanish Research Centres of Excellence (LCF/BQ/DI17/11620012). We thank the Andalusian Scientific Information Technology Center (CICA, Spain) for providing computational resources.

#### DATA AVAILABILITY STATEMENT

Sequence data are available from GenBank (see Table S1). Distribution data were sourced from GBIF and georeferenced herbarium specimens available in accessible herbaria (see Material and Methods). The alignments and full set of occurrence data used in this study can be downloaded from DRYAD (https://doi.org/10.5061/dryad.bnzs7h486).

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## BIOSKETCH

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Authors' contributions: I.L. & M.E. conceived the idea; J.G.D. & K.B. performed the laboratory work; M.E. & J.G.D. analysed the data. All authors contributed significantly to the final manuscript.

## SUPPORTING INFORMATION

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